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A giant member of the genus *Lobolytoceras* Buckman, 1923 (Ammonitina, Lytoceratinae) from the Oxfordian of SW Madagascar

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With 11 figures and 2 tables

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Abstract: We describe the giant lytoceratid taxon *Lobolytoceras costellatum* (Pavia, 2002) n. comb. from the Upper Jurassic (Oxfordian, "Rauracien") of SW-Madagascar and discuss the possible relation to the Toarcian (Early Jurassic) species "*Lytoceras*" *siemensi* Denckmann, 1887 as well as the systematic consequences. The stratigraphic range of the genus *Lobolytoceras* Buckman, 1923, hitherto only known from the Lower Toarcian will be extended to the Oxfordian-Tithonian (Upper Jurassic).

Key words: Ammonitina, *Lobolytoceras*, Jurassic, Rauracian, Madagascar, systematics, morphology.

1. Introduction

The ammonite-bearing Oxfordian deposits of the southern Morondava Basin of southwestern Madagascar are separated by Collignon (1959) into the lower "Argovian" of Early to early Middle Oxfordian age, dominated by Stephanoceratoidea (*Epimayaites, Prograyiceras*) and Perisphinctoidea (*Orinoides, Dichotomosphinctes*) associated with Phylloceratida (*Sowerbyceras, Ptychophylloceras, Phylloceras*), Haploceratoidea (*Proscaphites, Taramelliceras, Trimarginites, Lissoceras*) and Lytoceratina, and the higher "Rauracien" of late Middle to Late Oxfordian age. The diverse "Rauracien" ammonite fauna from the Sakaraha region, which also contains the giant lytoceratid species *Lobolytoceras costellatum*, is well preserved. Its shells remain still aragonitic (Lécuyer & Bucher 2006). The ammonites are enriched in slowly deposited thick-bedded Fe-oolithic limestones intercalated with *Exogyra*-coquinas and sandy clay- and mudstones of a near coastal (Uhmann 1996) to open shelf environment (Besairie & Collignon 1972). The geological setting of these deposits representing characteristic post-rift sediments that have been deposited after the active breakup phase of the Gondwana supercontinent into the western and eastern parts of Gondwana along the Davie transform fault zone during Toarcian/Aalenian is given by Geiger (2004). For some years, a large number of nautilids, ammonites, bivalves and gastropods, dug in special fossil pits of the Sakaraha region (Richter 2004), have been commercially distributed over the world. The Middle Oxfordian "Rauracien" ammonite fauna is dominated by representatives of the Ammonitina, particularly of different Haploceratoidea (*Taramelliceras, Lissoceras*), Perisphinctidae (*Divisosphinctes*, *Kranaosphinctes, Prososphinctes, Dichotomosphinctes, Lithacospinctes*), and Aspidoceratidae (*Euaspidoceras, Mirosphinctes, Epaspidoceras, Aspidoceras*, additionally in the Late Oxfordian Bimam-

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matum Zone less abundantly *Amoebopeltoceras* and *Epipeltoceras*). The more conservative ammonite groups are represented by both the phylloceratids (*Phylloceras, Holcophylloceras, Ptychophylloceras*) and lytoceratids. The most abundant lytoceratid ammonite is the small to middle-sized "*Hemilytoceras*" *fraasi* (DACQUÉ) (Fig. 3c-d). The macroconch (giant) lytoceratid taxon *Lobolytoceras costellatum* described here corresponds in its morphological features with the Liassic genus *Lobolytoceras* BUCKMAN, 1923 rather than with the also more or less similar "*Hemilytoceras*" SPATH, 1927 and *Metalytoceras* SPATH, 1927, as demonstrated below. We have compared these three similar lytoceratid genera (Fig. 11) and have finally emended the generic description for *Lobolytoceras* BUCKMAN, 1923.

Lytoceratid ammonites are generally characterised by a more or less evolute, i.e. a wide umbilicus and little or no overlapping of the whorls, and a thin-walled shell which is usually weakly sculptured. Only in some groups a simple ornamentation occurs, such as single ribs or bunges, occur, especially on the body chamber. Whorl section is typically round, laterally compressed or transversely elliptical. The primary suture formula is ELU_2U_1I (SCHINDEWOLF 1961), and the suture elements become strongly slit (microphyll), showing the following evolutionary trends:

• The bifid internal lobe (I) generates one or more lateral branches, the first one being the main branch, which becomes horizontal orientated (as do the other branches later on, too), thereby the I becomes typically cruciform in shape.

• Lateral lobes are trifid in the lowermost Liassic forms, becoming bifid in later forms.

The following four characters occurring in the lytoceratids are apomorphic for the group and do not occur in any other ammonoid group.

1. Fimbriate ornamentation of the ribs (ribs are denticulated on their basis) occurs for the first time in the Early Liassic group of *Lytoceras secernendum* DE STEFANI, 1887.

2. The flares of *Lytoceras* derived from plesiomorphic parabolic-ribs (e.g. in *Eolytoceras, Analytoceras*) already known for Early Triassic phylloceratid ancestors.

3. In some members of Cretaceous Lytoceratoidea the typical quinque-lobate primary suture becomes six-lobate and is therefore the most developed primary suture of all ammonoid groups (SCHINDEWOLF 1961).

Fig. 1. Sexually dimorphic couple of *Lobolytoceras siemensi* (DENCKMANN) from the Lower Toarcian of Altensittenbach near Hersbruck, Southern Germany: The microconch (4.0 cm) is preserved within the broken and mostly missing body chamber of the macroconch (diameter 10.4 cm), Coll. KEUPP PA-4409.

4. The septal lobe (Is) (YABE 1903) onsets ontogenetically about the fourth whorl in Jurassic and Cretaceous lytoceratid genera. The structure is generated by median dorsal septal recesses of the internal lobe (I) that are curved backwards into a short tube and attached on the septal surface of the preceeding septa. A funnel-shaped septate tunnel lying within the phragmocone on the dorsal part of the chamber is thus formed. The attached part of the septal lobe is fluted in a complex manner like that of the septal periphery in contact with the outer shell wall. It occurs during the early Liassic through the continuously backwards drifting of the internal lobe. The dorsal septal tunnel is conjunct with the ventral part of the chamber. This can be seen in an exact median section of the structure. In contrast to the recognised significance of the development of the septal apparatus for the ammonoid systematic, it is still remarkable that this phenomenon was little noted and not seriously investigated in a systematic way (see SCHINDEWOLF 1961-1968; SALFELD 1924).

For some lytoceratid members, a sexual dimorphism is described, particularly for "*Lytoceras*" *siemensi* (Keupp 1980; Riegraf et al. 1984). Some microconch genera (*Derolytoceras, Trachylytoceras*) are reported as sexually dimorphic pendants of the macroconch genus *Lytoceras* (Meister 1986; Rulleau 1998, 2006). In general, lytoceratid microconchs are smaller in diameter, with stronger ornamentation on the body chamber, sometimes with minor whorl expansion rates compared to their macroconch counterparts (Fig. 1).

The jaw apparatus is not completely known, but Schmidt (1928), Lehmann (1971), Lehmann et al. (1980) and Tanabe & Landman (2002) reported an Anaptychus for lytoceratid ammonites. This kind of jaws normally consists mostly of (black) scleroproteins; nevertheless, the Late Cretaceous *Gaudryceras* and *Tetragonites* showing substantial calcareous layers ("Rhynchaptychus") have been interpreted as a discrete evolutionary trend (Kanie et al. 1978; Tanabe et al. 1980; Tanabe & Fukuda 1983).

Following Guex (1995), (Guex et al. 2004) and Shigeta (2006), the Lytoceratoidea Neumayr, 1875 represent a monophyletic taxon of the order Ammonitida. The complex structure of the septal lobe and the fact that it only occurs in the Lytocerataceae Neumayr, 1875 leads us, unlike Arkell et al. (1957), to the assumption that all lytoceratid taxa with such a septal lobe can be combined into a monophyletic group.

Abbreviations: D = diameter in mm; Wh = whorl height in mm, Wb = whorl breadth in mm, Uw = umbilicus width in mm, Uw/D = in percent, WER = whorl expansion rate.

2. Systematic palaeontology

Superfamily Lytoceratoidea Neumayr, 1875
Family Lytoceratidae Neumayr, 1875
Subfamily Lytoceratinae Neumayr, 1875
Genus *Lobolytoceras* Buckman, 1923

Lobolytoceras costellatum (Pavia, 2002) n. comb.
Figs. 2-4

1871 *Lytoceras sutile* Opp. – Gemmellaro, p. 184, pl. 10, figs. 1-3.
1876 *Lytoceras sutile* Opp. – Gemmellaro, p. 31, pl. 5, figs. 1-3.
2002 *Metalytoceras* (?) *costellatum*. – Pavia, p. 96, figs. 52-53.

Locality: Sakaraha near Tulear, southwestern Madagascar.

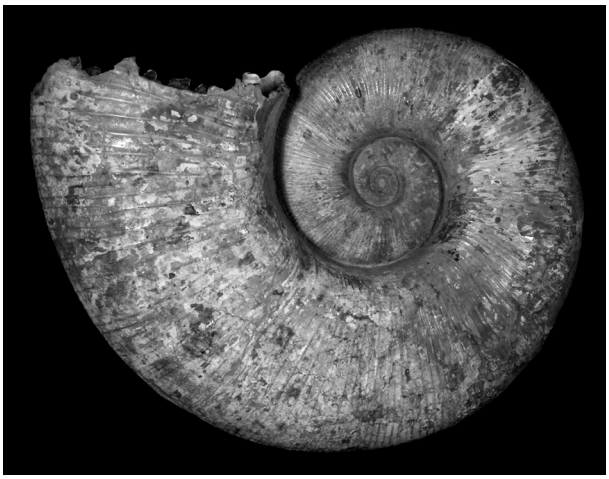


Fig. 2. *Lobolytoceras costellatum* (Pavia), "Rauracien", Sakhara, Madagascar; phragmocon of a giant macroconch with 620 mm diameter (MAn-3059, Coll. Keupp).

Stratigraphy: Late Middle Oxfordian (= "Rauracien" sensu Collignon 1959), accompanied with *Kranaosphinctes* (*Pachyplanulites*) *subevolutus* (Waagen), *Divisosphinctes besairiei* Collignon, *Prososphinctes virguloides* (Waagen). All specimens (Table 1) are housed at the collection H. Keupp, Institute of Geological Sciences at Freie Universität Berlin, under the given MAn-number.

Occurrence: Sicily, Madagascar.

Stratigraphic range: Oxfordian – Tithonian.

Tab. 1. Morphological features of all available specimens of *Lobolytoceras costellatum* (Pavia, 2002) n. comb. from the Keupp Coll.; MAn-1788 laterally depressed, MAn-1952 Wh slightly corroded.

Specimen	D	Wh	Wb	Uw	Wh/Wb	Uw/D	WER
MAn-3059	620	276	213	195	1.30	31.5	3.25
MAn-2038	220	103	77	66	1.34	27.7	3.54
MAn-1750	219	101.7	71.1	55.7	1.43	25.4	3.49
MAn-1871	209	96.7	69.3	54.2	1.40	25.9	3.46
MAn-1788	196	88.5	62.8	55.8	1.41	28.5	3.32
MAn-1752	158	73.6	52.5	44.6	1.40	28.2	3.50
MAn-1751	70.6	32.3	23.6	20.1	1.37	28.5	3.40
MAn-1952	70.1	32.7	24.3	20.4	1.35	29.1	3.51

Description: Macroconch with moderately evolute coiling. Section of the last whorl highly oval (Wh/Wb about 1.35), laterally compressed, with rounded venter, rounded umbilicus shoulders and umbilicus walls (Figs.

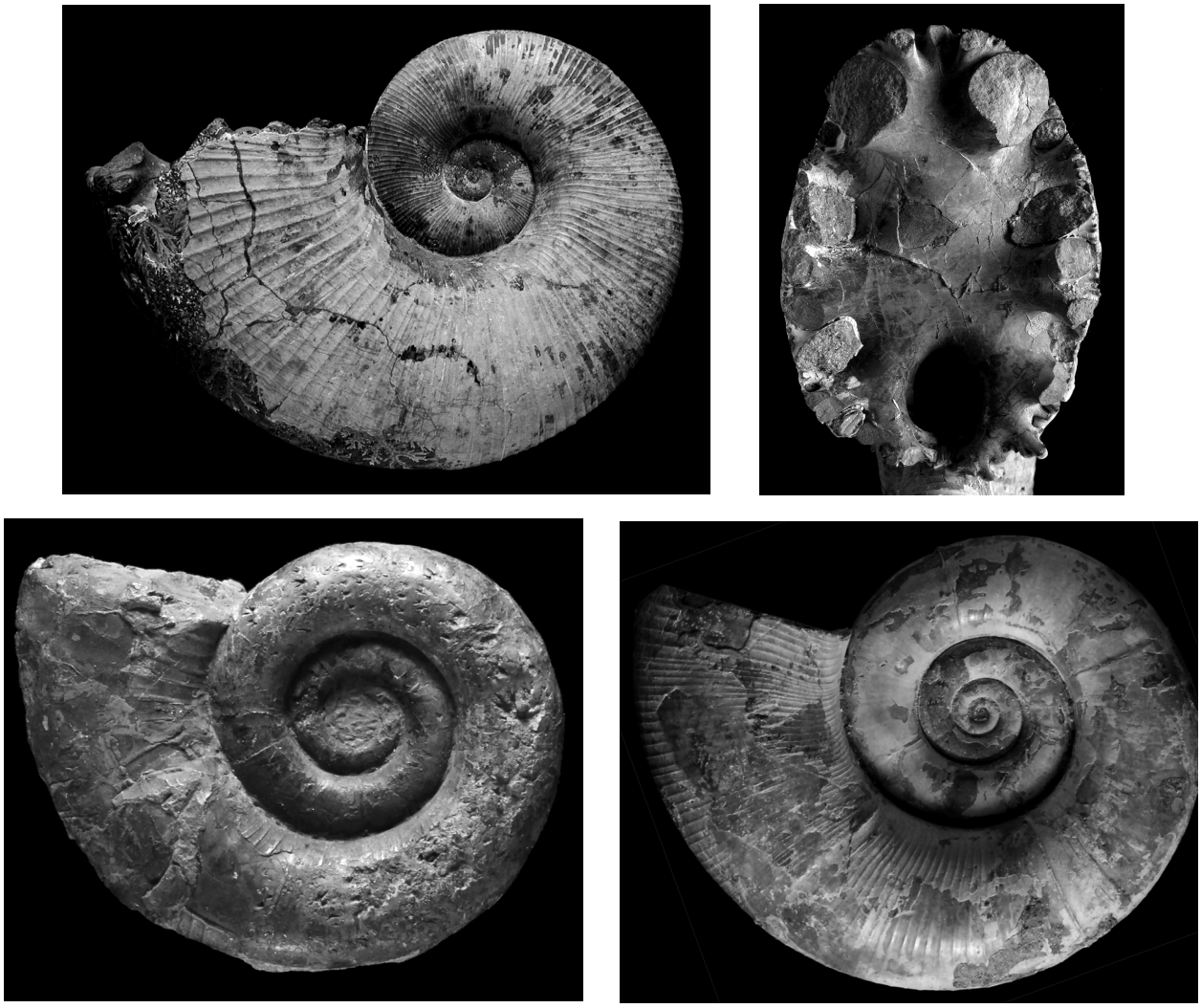


Fig. 3. Top left: 220 mm large specimen MAn-2038 of *Lobolytoceras costellatum* (Pavia); top right: showing the whorl section with a great deepening in the ventral region caused by the backwards drifting of the internal lobe which is partly attached to the preceding septum, forming the septal lobe – for the first time recorded for this species and genus. Bottom left: *Lytoceras fraasi* Dacque, 1910, holotype, Oxfordian of Mombasa, Kenya, with 52 mm in diameter (housed in the collection of the Staatliches Museum für Naturkunde, Stuttgart; Col. No. 21433); bottom right: *Lytoceras fraasi* from Sakhara, Madagascar (MAN-2031, Coll. Keupp), 71 mm in diameter.

2-3). Shell with a high whorl expansion rate about 3.4. Ribs are moderately concave on the lower 1/3 of the flank, becoming slightly convex on the middleflank and crossing the ventral region without weakening. Neither constrictions nor flares observed on the shell, but stronger ribs with weakly fimbriate ornamention occur irregularly. Fimbriate ornamention only occurs on back side of the stronger ribs. Internal mould covered with six to seven feeble varices per 1/2 whorl. Shell surface with very fine strigation which can easily be seen in streak of light. Ribs are bifurcating at a very acute angle in different positions on the flank. Ribbing of inner whorls consists of simple or bifurcated but smooth and non-fimbriate, slightly sinuous ribs. The internal lobe is generating a septal lobe, which is frilled like the suture line (Hoffmann & Keupp 2007). The appendages of the septal lobe, which are attached on the preceding septum, build a brush-like structure that reaches 1/3 of the whorl high in larger specimens (Fig. 4).

The highly complex first lateral lobe is bifid, its external branch nearly reaching the siphuncle region in adult specimens. The external lobe becomes thereby clearly shorter than the L (Fig. 6).

Discussion: Our specimens from Madagascar correspond morphologically to "*L.*" *sutile* (= *Metalytoceras* (?)

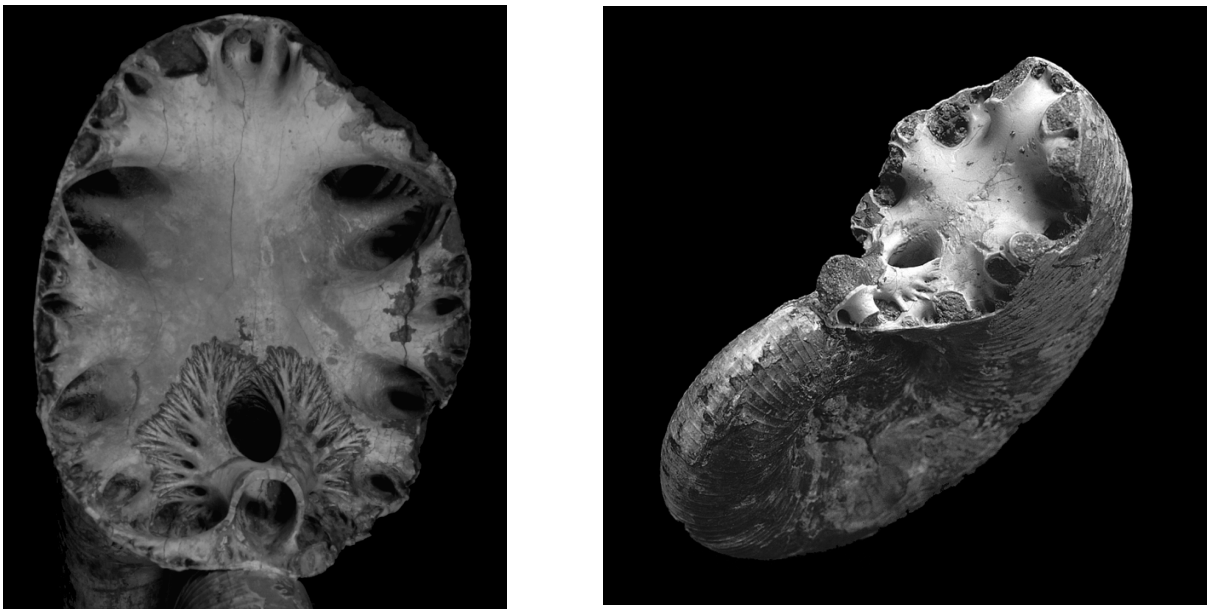


Fig. 4. Left: Adult macroconch of *Lobolytoceras costellatum* from the Oxfordian of Sakhara, Madagascar (MAn-3059, Coll. Keupp, diameter 620 mm). Right: Juvenile specimen (MAn-1751, Coll. Keupp, diameter 7.1 cm) of *Lobolytoceras costellatum*; demonstrating the ontogenetic modification of the septal lobe.

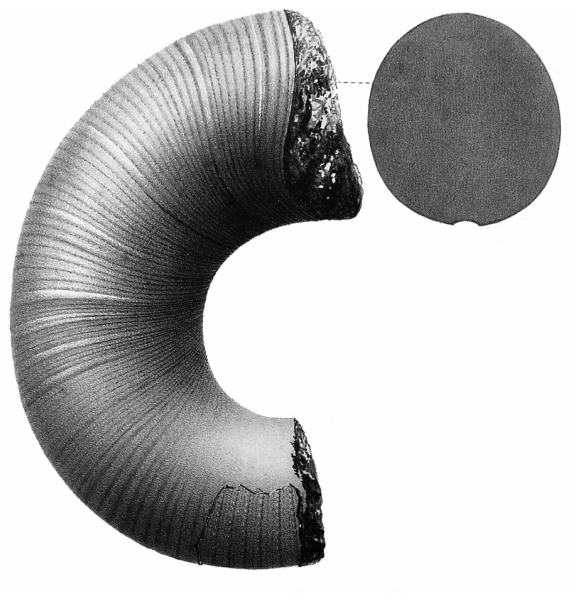


Fig. 5. Type material of *Lytoceras sutile* showing a part of the body chamber with aperture and the non-bifurcated ribs, and Wh/Wb ratio; refigured from Zittel (1868, pl. 12, fig. 1a-b), diameter is approximately 200 mm.

costellatum Pavia, 2002) and resemble *Lobolytoceras siemensi* Denckmann, 1887. Gemmellaro (1871, 1876) identified a specimen incorrectly as *Lytoceras sutile* from the Tithonian (Upper Jurassic) of the South of Palermo that looks similar to our Oxfordian specimen. The Gemmellaro Collection has been taxonomically revised since then and the specimen was reclassified by Pavia (2002) as *Metalytoceras* (?) *costellatum*.

The true *Lytoceras sutile* was briefly described by Oppel (1865) as very similar to *Ammonites francisci* (Hauer 1856, pl. 22, figs. 1-2), but differs from *Am. francisci* because of its weak and dense ribs, and the more ventrally depressed section of the last whorl. In Zittel (1868), the non-bifurcated ribs of *L. sutile* are irregularly spaced and rursiradiate on the lower flank, becoming prorsiradiate in the middle and upper parts of the flank (Fig. 5). As already discussed in Pavia (2002), only the figure in Zittel (1868, pl. 12, fig. 1) represents the lectotype of *Lytoceras sutile* (fide Patrulius and Avram 1976: 163, see also Zeiss 2001). Therefore, Roman (1938) was erroneous in regarding the complete specimen figured by Zittel (1870) as the (lecto)type of Oppel's taxon. Its measurements taken from Zittel (1868, pl. 12, fig. 1a-b):

D = 151.1mm, Wh = 57.1mm, Wb = 52.4mm, Uw = 51.8mm (34.3 %); WER = 2.58.

Because of the rounded whorl section of its very advolut shell, and the lower whorl expansion rate, the dense ribbing and the fine fimbriate ornamention of the simple ribs *Lytoceras sutile* represents a typical member of the "*Hemilytoceras*"-group (Fig. 5).

In accompaniment with Zeiss (2001), we include the following species into the subgenus "*Hemilytoceras*", which is a subjective junior synonym of *Lytoceras* Suess, 1865 (see below), in respect to the illustrations in Zittel (1868): *Lytoceras montanum* (Oppel, 1865); *L. liebigi* (Oppel,

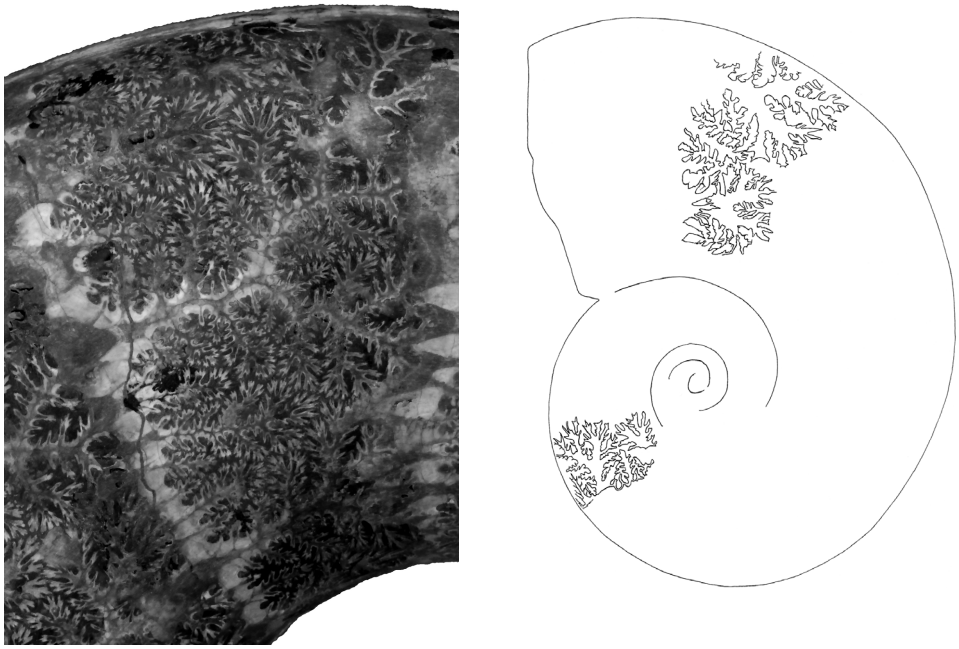


Fig. 6. Left: *Lobolytoceras costellatum* (Pavia), Oxfordian of Sakhara, Madagascar (Wh at about 80 mm, MAn-1871, Coll. Keupp). Right: Reproduction of Buckman's (1923) figure of *Lobolytoceras siemensi* with 60 mm in diameter showing the similar general morphology of the L lobe.

1865), *L. sutile* (Oppel, 1865), and *L. immane* (Oppel, 1865). *Lytoceras liebigi* var. *strambergensis* Zitteel was synonymized with *Lytoceras immane* by Sapunov (1979), see Zeiss (2001).

Pavia (in Pavia et al. 2002) introduced the Tithonian lytoceratid *Metalytoceras* (?) *costellatum*. After his diagnosis and morphological description (Pavia et al. 2002: 97), this form fits very well with our Oxfordian material from Sakhara: Both share the oval whorl section, lateral compression, with a high growth rate. The shell is covered with very fine irregular bifurcating ribs. Neither constrictions nor flares are visible on the shell surface. There is a suture line with deeply subdivided accessories of S1 and short L1. Our giant Oxfordian species shares the bifurcating ribs and the high-oval whorl section, the lack of flares, and the gentle fimbriate ornament with *Metalytoceras*, but differs, from this genus due to its higher whorl expansion rate, its irregular bifurcation of the ribs in different positions on the flanks, and by having a smaller umbilicus, as does *Metalytoceras* (?) *costellatum* from Sicily. Therefore, we cannot follow Pavia's (2002) classification of Gemmellaro's "*Lytoceras sutile* Opp." as a presumed member of the genus *Metalytoceras* Spath, 1927. We suggest the macroconch of *Lobolytoceras siemensi* (Denckmann, 1887) from the Jurassic (Early Toarcian) as the most similar morphotype. *Metalytoceras* (?) *costellatum* Pavia, 2002 and our Oxfordian specimen share the following characters with *Lobolytoceras*:

(1) Due to high growth rate the whorl section is strongly compressed (at least 5-6 percent more than the value of Wh in *L. sutile*);

(2) narrower umbilicus than in the coeval *L. montanum* and *L. sutile*;

(3) bifurcating ribs on the flanks;

(4) fine riblets with denticulations; and

(5) lack of constrictions on the outer shell surface.

For the two taxa, a similar Uw/D ratio, Wh/Wb ratio, and whorl expansion rate is reported (Fig. 11) but no varices have been reported for *L. siemensi*. The lateral lobe is also of similar morphology in *Lobolytoceras siemensi* and *Lobolytoceras costellatum* from the Oxfordian of Madagascar, but is more complex in the latter (Fig. 6). The suture line of the *Lobolytoceras costellatum* (Pavia, 2002) from the Tithonian is unknown. As a result, we reject the theory of Pavia (2002), who deviated *Metalytoceras* via *L. montanum* from *Lytoceras* s. s., and suggest to combine the Toarcian "*Lytoceras*" *siemensi*, the Tithonian "*Metalytoceras*" (?) *costellatum*, and the specimen from the Oxfordian of Madagascar together into the genus *Lobolytoceras* Buckman, 1923.

Generic remarks: Pavia (2002) regarded misleadingly in our opinion Gemmellaro's specimen as a probable *Metalytoceras* Spath, 1927. To underline that Pavia's species does not belong to the genus *Metalytoceras* we give a short characterisation for this genus.

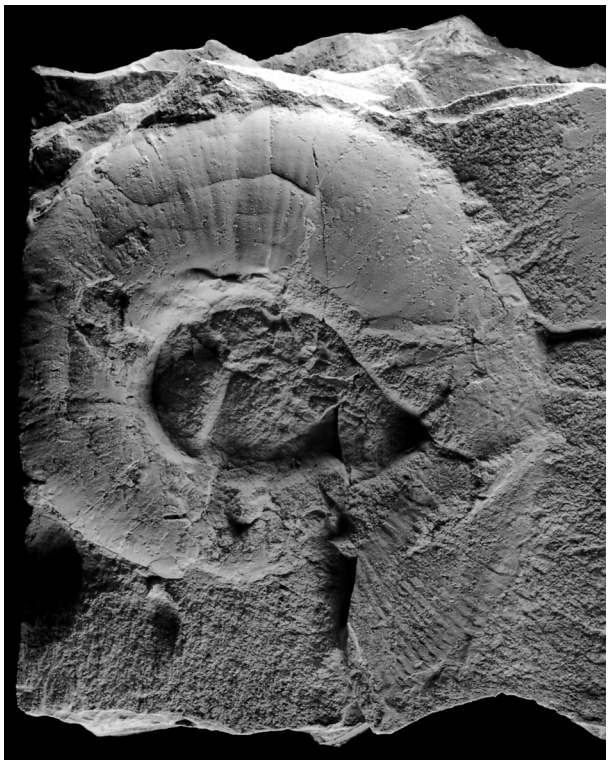


Fig. 7. Feeble constrictions and the regularly bifurcated ribs are scarcely visible on the holotype of *Metalytoceras triboleti* (Hohenegger in Uhlig 1901, pl. 1, fig. 1), diameter about 74 mm. The holotype is housed in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Col. No. AS III 149.

Genus *Metalytoceras* Spath, 1927
Fig. 7

Type species: *Lytoceras triboleti* Hohenegger in Uhlig 1901, p. 22, pl. 1, figs. 1a-b, 2, 7 (non Hohenegger in Uhlig, 1883), originally designated by Spath, 1927. Holotype re-figured here as Fig. 7.

Description: The type specimen is characterised by weak, radial, irregular and distant constrictions (i.e. not more than 5 constrictions per whorl) visible on both the internal mould and shell of adults. From the inner whorls, no constrictions are reported. The radial ribs are very fine on inner whorls and closely spaced (e.g. 31 ribs between two constrictions, i.e. 1/4 of the whorl) on outer whorl, with a slightly sinuous direction. As a typical character, the ribs are regularly bifurcate and rarely trifurcate on the outer flanks at a very acute angle (Fig. 7). No flares, no parabolic lines/ribs, and no ventral median keel is reported for the genus. Ventral ornamentation consists of finely split, fimbriate riblets. Fimbriate ornamentation does not exist on the ribs of lower flank. In adult specimens, the whorl section is higher than wide, with flattened, slightly convex flanks and a rounded venter. The umbilicus is small. The suture line is characterised by an external lobe nearly as deep as the first lateral lobe. All lateral lobes are bifid.

Measurements: Taken from Uhlig 1901, pl. 1, fig. 2: D = 74.2mm (reconstructed), Uw = 27.9mm (37.6%), h = 25.7mm; WER = 2.34

Remarks: When Spath (1927) erected the genus *Metalytoceras* he designated *Lytoceras triboleti* Hohenegger in Uhlig (1901) as its type species. The original figure was reproduced and touched up slightly in Arkell (1957) where the genus was reported with a question mark. The validity of the genus was emphasised by Kennedy & Klinger (1978: 259): "..., and is readily separable from *Lytoceras* by virtue of the consistent splitting of the ribs into fine riblets over the venter". In contrast to the foresaid authors Vašicek (1975) stated that Uhlig's material was morphologically insufficient to determine a new genus for it. For the genus, no septal lobe has been yet described, but is highly probable to exist in a well developed state. Notwithstanding that the suture line is unknown, we state that this genus is valid because of its unique combination of morphological features described above.

In the revision of the Gemmellaro Collection, Pavia (2002) stated that it is worth noting that the hypothesis expressed by Uhlig (1901), Spath (1927) and Roman (1938), i.e. to connect the genus *Metalytoceras* to the Pliensbachian group of *Kallilytoceras villae* (Meneghini), is unacceptable even if the two genera are similar in density and regular bifurcated riblets. In fact, *Kallilytoceras* shows a subquadratic whorl-section and clearly denticulate riblets. The morphologically most correlated form of the *Kallilytoceras* group is *K. ovimontanum* Geyer, 1893 (cf. Geyer 1893, pl. 8, fig. 1a-c).

Unlike in *Metalytoceras*, the *K. ovimontanum* displays its maximum whorl width near the umbilicus edge, possesses a straight umbilicus wall that is slightly nutant in adult stage, and a higher involution (1/5 of the preceding whorl). Ribs are very irregular, from fine and dense to coarse and distant. The ribbing is alternating and compounding, ribs are biconcave and slightly prorsiradiate, frequently bifurcating and slightly fimbriate (Geyer 1893; Wiedemayer 1977).

Because of Gemmellaro's misidentification of his specimen as a *Lytoceras sutile*, the true *L. sutile* is now grouped in the genus "*Hemilytoceras*", as mentioned above. We will give a short description for "*Hemilytoceras*".

Genus "*Hemilytoceras*" Spath, 1927
(= junior subjective synonym of *Lytoceras* Suess, 1865)

Type species: "*Hemilytoceras*" *immane* (Oppel) in Neumayr, 1883 originally designated by Spath (1927). (Synonyms: *Ammonites atrox* Oppel, 1865 and *Lytoceras liebigi* var. *strambergensis* Zittel, 1868).

Stratigraphy: Tithonian – Lower Cretaceous (Valanginian) of Silesia.

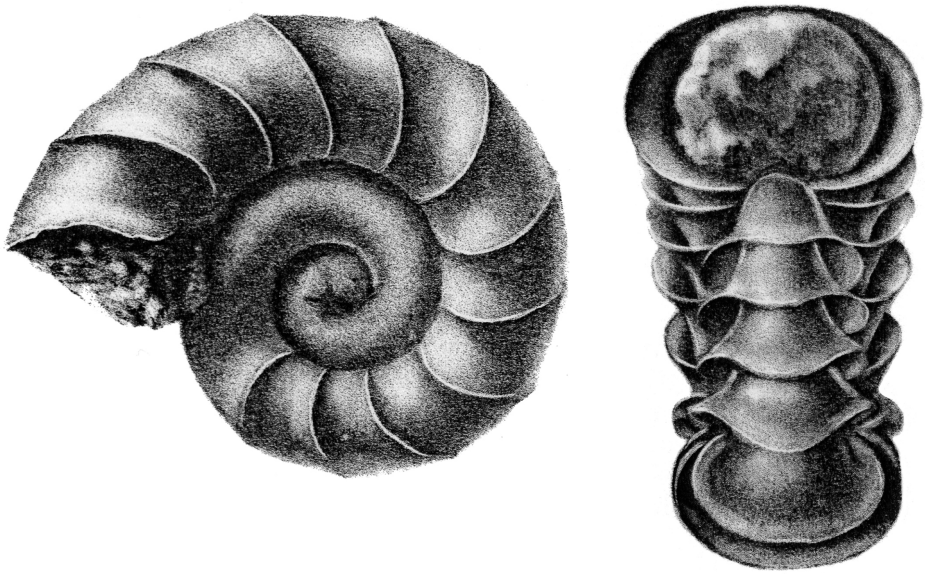


Fig. 8. Original drawing of "*Hemilytoceras*" *immane*, the type species of this genus (from NEUMAYR, 1883), with the reconstructed trumpet-like flares; dimensions unknown.

Description: Inner whorls round and smooth, outer whorls becoming depressed and in some developing high lamellae which bend forward on the venter (ARKELL 1957). No bifurcating ribs are visible in ZITTEL (1868, pl. 11, figs. 1-3) where he figured *Lytoceras liebigi* var. *strambergensis* (Fig. 9). Constrictions are absent. The original description of the type species by OPPEL (1865: 551) is as follows: *Ammonites immanis* is very similar to *Lytoceras liebigi* OPPEL, but differs in orientation of the smooth denticulate, flatter ribs. The ribs are more prorsiradiate over the broad venter than in *Lytoceras liebigi* and on the latest part of the body chamber building high, lamellar-like widely spaced flares, whereas KENNEDY & KLINGER (1978) observed high, concave and closely spaced lamellar flares.

To extend the idea of the *Ammonites immanis* OPPEL, we are adding original descriptions of closely related forms from the Tithonian and refigure the type species as designated by SPATH (1927), figured in NEUMAYR (1883) (Fig. 8).

Ammonites liebigi OPPEL is very close to *Ammonites cornucopiae* in relation to the whorl expansion, but differs in its ornamentation, which consists of finer ribs that first appear at a diameter of 30 mm. Inner whorls covered with irregular widely spaced ribs. A detailed description of the flare-structure was given by NEUMAYR (1883) and BESNOSSOV (1958) for the genus. NEUMAYR (1883) characterised *Lytoceras immane* by an aperture widening out into a trumpet shape (Fig. 8). BESNOSSOV (1958) added a classification of different flare types. The flares of *Lytoceras immane* are of thysanoceratid type i.e. flares first occur in later ontogenetic stages (5th or 6th whorl); they are smooth and thick and associated with constrictions. Flares are not so great on the venter but with maximum height on the flanks. The flares are tilted forward and denticulate only at the basis.

Measurements: Taken from NEUMAYR (1883, fig. 2): D = 50.53 mm, Uw = 22.42 mm (44.4 %), Wh = 17.15; WER = 2.29.

Remarks: SPATH (1927) stated that *Hemilytoceras* and *Pterolytoceras* SPATH, 1927 differ considerably in their ornamentation and especially in the type of flares, also in their suture lines. The genus *Pterolytoceras* SPATH, 1927 is somehow related to "*Hemilytoceras*" SPATH, 1927 as recognised by COLLIGNON (1960) and ZEISS (2001), but for its generic description (enlarging slowly, surface covered with minute crinkled growth lines and fine irregular ribs and flares, whorl section subcircular i.e. higher than wide) given by ARKELL (1957), it could be excluded as a possible relative of *Lobolytoceras costellatum*. However, for the lack of apomorphic characters, we are forced to include "*Hemilytoceras*" into the variable group of *Lytoceras*.

Finally, according to the lack of a diagnosis in BUCKMAN (1923) and the insufficient description in ARKELL (1957), we present the following emended diagnosis for the genus *Lobolytoceras*, which is based on the original description of the type species *Lytoceras siemensi* DENCKMANN, 1887.

Genus *Lobolytoceras* BUCKMAN, 1923
Fig. 10

Type species: *Lytoceras siemensi* DENCKMANN, 1887, p. 42 (156), pl. 1, fig. 8a-b; holotype re-figured here in Fig. 10. Non *Lobolytoceras perlobulatum* BUCKMAN, 1924, pl. 440.

Included species: *Metalytoceras*? *costellatum* PAVIA, 2002; *Lobolytoceras perlobulatum* BUCKMAN, 1924; *Lytoceras siemensi* DENCKMANN, 1887.

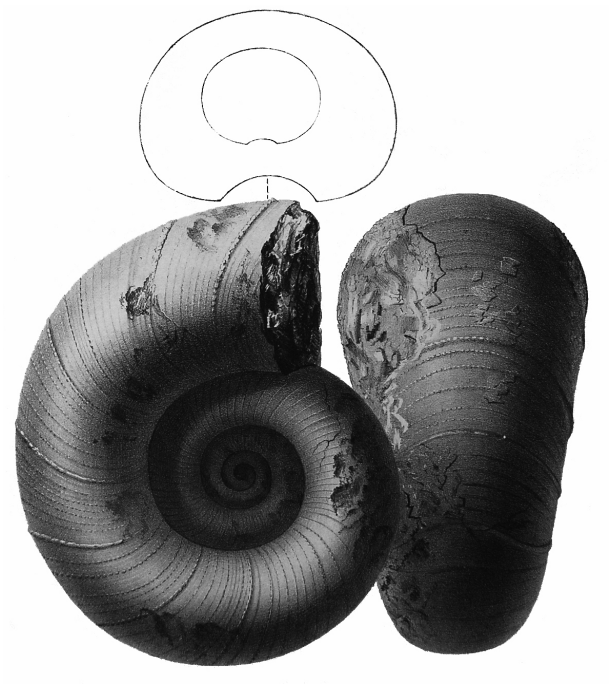


Fig. 9. Part of the original plate 11, figs. 1c, 3a-c in Zittel (1868) showing the characteristic Wh/Wb ratio of "*Hemilytoceras" immane*; specimen is about 200 mm in diameter.

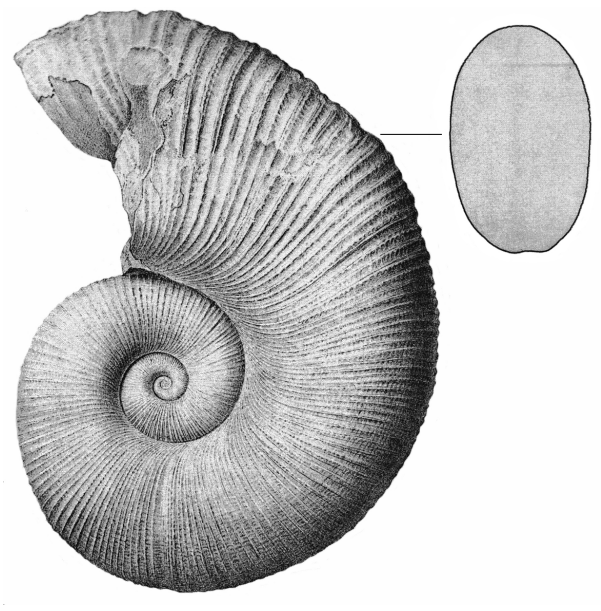
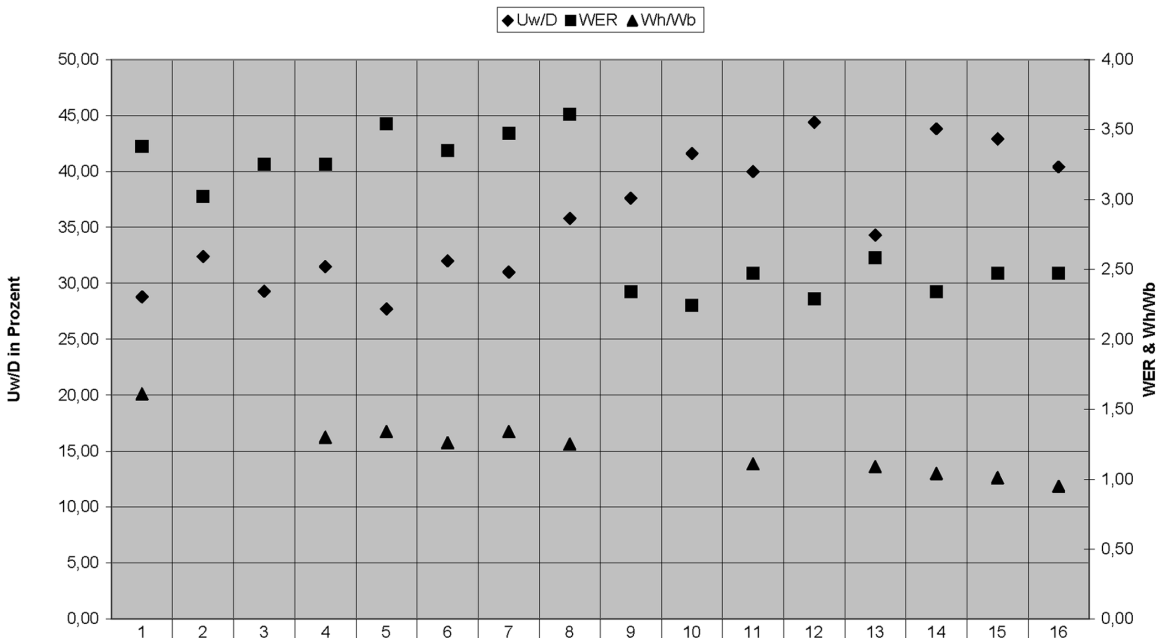


Fig. 10. Holotype of *Lytoceras siemensi* Denckmann, 1887 (= type species of *Lobolytoceras* Buckman, 1923) with bifurcating fimbriate ribs and strigation visible on the outer whorl. Top right: High oval whorl section of the type species; diameter of the specimen is 184 mm.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
◆Uw/D	28,80	32,40	29,30	31,50	27,70	32,00	31,00	35,80	37,60	41,60	40,00	44,40	34,30	43,80	42,90	40,40
■WER	3,38	3,02	3,25	3,25	3,54	3,35	3,47	3,61	2,34	2,24	2,47	2,29	2,58	2,34	2,47	2,47
▲Wh/Wb	1,61			1,30	1,34	1,26	1,34	1,25			1,11		1,09	1,04	1,01	0,95

Fig. 11. Morphological relations between the taxa discussed in the text; data taken from Table 2.

Tab. 2. Morphological features discussed in the text for *Lobolytoceras, Lytoceras, Metalytoceras* and *Kallilytoceras*.

No.	Specimen	diameter in mm	Wh in mm	Wb in mm	Uw in mm	Uw/D in %	WER	Wh/Wb
01	*Lobolytoceras siemensi* (Denck., 1887, macroconch, pl. 1, fig. 8, 8a)	184	84 (71.9)	? (44.7)	53	28.8	3.38	1.61
02	*Lobolytoceras siemensi* (Denck., 1887: pl. 1, fig. 5, microconch)	29.0	12.3	?	9.4	32.4	3.02	?
03	*Lobolytoceras siemens*i (Buckman 1923: pl. CDXL)	184	82	?	54	29.3	3.25	?
04	*Lobolytoceras costellatum* (MAn-3059, Coll. Keupp)	620	276	213	195	31.5	3.25	1.30
05	*Lobolytoceras costellatum* (MAn-2038, Coll. Keupp)	220	103	77	61	27.7	3.54	1.34
06	*Lobolytoceras costellatum* (Pavia, 2002, holotype, p. 96, figs. 52-53)	62.2	28.2	22.3	19.8	32	3.35	1.26
07	*Lobolytoceras costellatum* (Pavia, 2002, p. 96)	91.3	42.3	31.6	28.2	31	3.47	1.34
08	*Metalytoceras triboleti* (Uhlig 1901)	74.2	25.7	?	27.9	37.6	2.34	?
09	*Lytoceras fimbriatum* (Arkell 1957, fig. 225.3 a-b)	56.7	18.8	?	23.6	41.6	2.24	?
10	*Lytoceras fimbriatum* (Wiedmann 1970, pl. 6, fig. 7)	27.5	10	9	11	40.0	2.47	1.11
11	*Lytoceras immane* (Neumayr 1883, pl. 20, figs. 2-3)	50.5	17.2	?	22.4	44.4	2.29	?
12	*Lytoceras sutile* (Zittel 1868, pl. 12, figs. 1a-b)	151.1	57.1	52.4	51.8	34.3	2.58	1.09
13	*Kallilytoceras ovimontanum* (Geyer 1893, pl. 8, fig. 1a-c)	95	45	36	34	35.8	3.61	1.25
14	*Lytoceras fraasi* (MAn-2036, Coll. Keupp)	49.6	17.2	16.5	21.7	43.8	2.34	1.04
15	*Lytoceras fraasi* (MAn-2032, Coll. Keupp)	48.7	17.7	17.6	20.9	42.9	2.47	1.01
16	*Lytoceras fraasi* (MAn-2061, Coll. Keupp)	138.5	50.4	53.2	56.0	40.4	2.47	0.95

Emended diagnosis: Rounded inner whorls with rapid whorl growth rate of the later whorls in the kind that the body chamber is of the same diameter like the inner whorls. Later whorls with lateral compression that tends to result in an extraordinary Wh/Wb ratio. Shell covered with fine and delicate frequently bifurcating ribs, which are rursiradiate at lower flank and radial at the middle to upper flank. Strigation appears from the third whorl on, and becoming stronger on the body chamber, which looks therefore cancelated. The peristome is somewhat sinuous. Neither flares nor constrictions occur (Fig. 10).

The currently presumed microconch with coarser ribs of the body chamber (which do not exist on inner whorls of the macroconchs) is described and figured by Denckmann (1887: pl. 1, fig. 5) as a juvenile specimen.

Stratigraphy: Toarcian, Tenuicostatum Zone (Lower Jurassic) of Germany.

Remarks: As a typical difference between *Lobolytoceras siemensi* and *Lytoceras fimbriatum* (SOWERBY) DENCKMANN (1887), cited the round whorl section, a different whorl expansion rate, and flares for the latter. BUCKMAN (1923) chose *Lytoceras siemensi* DENCKMANN, 1887 as type species for his genus *Lobolytoceras*, but a generic description is lacking (see ZEISS 1974 for discussion), bifurcating ribs and strigation starting from the third whorl are also not to be found in the diagnosis given by ARKELL (1957). In 1924, BUCKMAN (pl. CDXL*, figs. 1-2) figured *Lobolytoceras perlobulatum*, which is identical with *Lobolytoceras siemensi* figured on pl. CDXL, figs. 1-2.

The genus *Lobolytoceras* is separated from *Lytoceras* by the significant morphological differences mentioned above. It might be possible for us to combine *Lobolytoceras costellatum* from the Oxfordian to the Toarcian genus "*Lobolytoceras*" with *L. siemensi* as ancestor and with GEMMELLARO's specimen from the Tithonian. A microconch is recorded only for the type species of the genus *Lobolytoceras* BUCKMAN, 1923 (see above). Referring to the missing constrictions in both the original description of DENCKMANN (1887) and ARKELL (1957), we suggest changing the systematic position of *Lobolytoceras* from Alocolytoceratinae to Lytoceratinae.

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